Differences in Inhalant Siphonal Papillae among the Japanese Species of Corbicula (Mollusca : Bivalvia)

Harada, Eiji; Nishino, Machiko

Differences in Inhalant Siphonal Papillae among the Japanese Species of *Corbicula* (Mollusca: Bivalvia)

EIJI HARADA

Seto Marine Biological Laboratory, Kyoto University,
Shirahama, Wakayama 649–22, Japan

and

MACHIKO NISHINO

Lake Biwa Research Institute of Shiga Prefecture,
Uchidehama, Otsu, Shiga 520, Japan

With Text-figures 1–10, Tables 1–3 and Appendix Table

Abstract Three common species of Japanese *Corbicula* are shown to differ in their morphology of the inhalant siphonal papillae. They are predominantly simple and least in number in freshwater *Corbicula leana*, predominantly simple but more numerous in brackish *Corbicula japonica*, and variable in shape and decisively most numerous in *Corbicula sandai* of Lake Biwa-ko. *Corbicula insularis* from Shirahama and *Corbicula fluminea* from Hong Kong are also compared. Shell morphometries are provided for the representative samples of four species from Japan. The taxonomy of the three Japanese species is reviewed briefly.

Key words: *Corbicula*, shell morphometry, siphon, inhalant siphonal pappillae, Lake Biwa-ko

Introduction

The Japanese species of *Corbicula* are currently assigned to *Corbicula leana* Prime, 1864, *Corbicula japonica* Prime, 1864 and *Corbicula sandai* Reinhardt, 1878 (Habe, 1977). They are distinguished from each other by morphological characteristics of the shell, but are also known to differ in breeding habit, i.e., monoecious and nursing newly hatched larvae in brood pouches in *C. leana*, but not in other two, and in habitat, i.e., *C. leana* in freshwater streams and ponds, endemic *C. sandai* only in Lake Biwa-ko and its tributaries and *C. japonica* widely in estuaries and brackish lagoons in Japan. Through a karyological study of these three species, Okamoto and Arimoto (1986) clarified their different, specific numbers of chromosomes. Takayasu *et al.* (1986) made a detailed morphometric analysis of the shell and confirmed the differences among the three species. However, young shells of the species are difficult to distinguish between.

During the course of our ecological investigation on *C. japonica* and *C. sandai*, we noticed remarkable differences in the shape and number of the inhalant siphonal papillae between them. In the present paper, the specific features of the inhalant siphonal papillae are described and examined for the three species of Japanese

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Corbicula, and the classification of Japanese *Corbicula* is reviewed briefly.

Recently, Masuda & Habe (1988) reported the occurrence of *Corbicula insularis* Prime, 1867, from a canal in Tsureshima, Kurashiki, near Okayama in western Honshu. On examining the *Corbicula* specimens collected from a ditch at Sakae, Shirahama, by Mr. H. Tanase in 1989, many of them were identified to this species from their shell morphology. Specimens of *Corbicula fluminea* (Müller, 1774) sent from Professor B. Morton in Hong Kong were given to us by Dr. H. Nakamura. These species are included in our examination for comparison.

Table 1. Species, localities and dates of collection of the specimens examined (in the order of the number of specimens examined respectively for species).

Species	Locality	Date
Corbicula leana	Lake Nishi-no-ko, Shiga	September 1985
	a canal, Gion, Okayama	September 1979
	River Aku-gawa, Shirahama, Wakayama	February 1986
	a ditch, Hatasho, Shiga	September 1985
	a brook, Hikone, Shiga	September 1985
	a ditch, Uraji, Tanabe, Wakayama	September 1989
	a ditch, Haya, Tanabe, Wakayama	October 1989
	a ditch, Tanoi, Hiki, Wakayama	November 1989
	a ditch, Sakae, Shirahama, Wakayama	November 1989
	River Minabe-gawa, Minabe, Wakayama	January 1988
	River Tonda-gawa, Shirahama, Wakayama	March 1985
	River Yumesaki-gawa, Hyogo	October 1985
Corbicula japonica	Lake Shinji-ko, Shimane	July - September 1985
	River Kushida-gawa, Mie	October 1985
	River Takase-gawa, Shirahama, Wakayama	November 1985
	Lake Kahoku-gata, Ishikawa	October 1985
	Lake Jyusan-ko, Aomori	June 1985
Corbicula sandai	Lake Biwa-ko, Shiga	June - December 1985
Corbicula insularis	a ditch, Sakae, Shirahama, Wakayama	November 1994
	ditches, Sakae, Shirahama, Wakayama	October 1994
	a ditch, Sakae, Shirahama, Wakayama	April 1995
	a ditch, Sakae, Shirahama, Wakayama	1989
Corbicula fluminea	New Territory, Hong Kong	unknown

Materials and Methods

Species, localities and dates of collection of the specimens examined are listed in Table 1. The specimens were identified to species, based on the shell morphologies currently provided in the relevant literature. It should be noted that the present study did not aim at a thorough morphological and taxonomical scrutiny of Japanese *Corbicula*, but rather intended to elucidate notable morphological difference among the species, and specimens from the historical localities, from where once specimens were recorded as distinct species, are not deliberately collected and included.

The specimens examined were alive or fixed and preserved in 5% formalin. Anaesthetizing the live specimens for fixation of the soft body in a relaxed state and for taking photographs of the extended siphon was tried with various chemicals and treatments, but was usually unsuccessful. The siphons were excised from the live or fixed specimens of various sizes for each species and were examined under a stereoscopic microscope. The shape, colour and arrangement of the papillae of the inhalant siphons were noted. Shell length, width and height were also measured on numerous specimens of all sizes from various localities for each species for comparison with the morphometries treated in previous works and for conventional confirmation of the species identity.

Results

Shell Morphometries

The shells of representative specimens of the Japanese species are shown in Fig. 1, and the hinge plates of the valves are illustrated in Fig. 2. Classical allometric relationships of shell height and shell width on shell length are presented for representative populations of four species in Fig. 3. Correlation coefficients are generally high for all local samples examined. The regression analyses yielded the results that the samples of four species differed from each other statistically significantly, not only among the species but also within a species. The only exception that no significant differences were shown was between the sample of Tanabe of *C. leana* and the sample of River Kushida-gawa of *C. japonica*, the number of specimens of which were both small. Nonetheless, four species are more or less separated in the slopes, in general accordance with the overall trends commonly advocated (cf. Takayasu *et al.*, 1986), i.e., that *C. sandai* is distinctly taller and thicker than *C. japonica* and *C. leana* and that *C. insularis* is thicker than *C. leana*. Kawashima *et. al.* (1989) reported for *C. japonica* that the slope for shell height on shell length was significantly larger in the population of River Kando-gawa than in that of Lake Shinji-ko; however, no significant difference was shown between the samples of River Kushida-gawa and Lake Shinji-ko in this study.

The specimens of *C. insularis* are rather unmistakably distinguishable from those of other three species in the shell coloration of pale yellow with a dark irregular pattern outside and of generally white with purple marks at ridges bearing the lateral teeth inside. They were found in a collection from a ditch for agricultural irrigation in Sakae, Shirahama, by Mr. H. Tanase in 1989, together with *C. leana* almost equally in abundance. The occurrence of *C. insularis* has been confirmed to be common in ditches in the neighbouring area. These represent presumably the second record of this species in Honshu, Japan, after the first record by Masuda & Habe (1988), and suggest the extended establishment of the populations of this originally Formosan species, which is suspected to be an ecomorph of *C. leana* by Morton (personal communication).

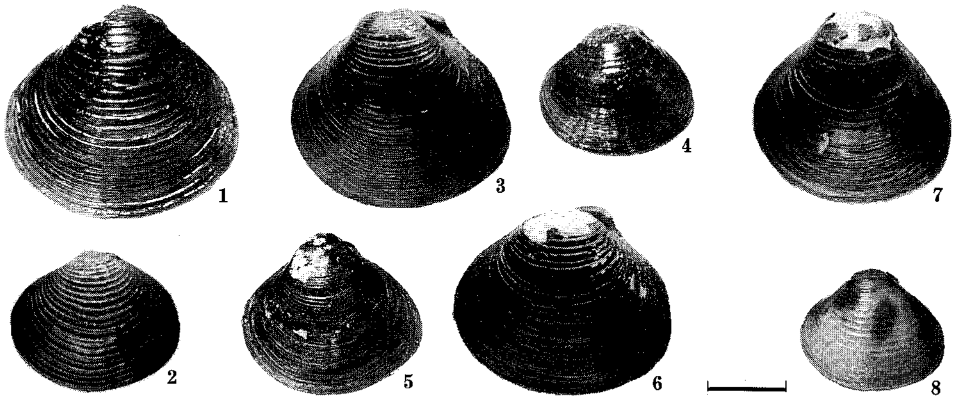


Fig. 1. Specimens of *Corbicula* from several representative localities in Japan, viewed from the left side. 1: *Corbicula leana* Prime, 1864, from a ditch in Haya, Tanabe; 2: *Corbicula leana* Prime, 1864, from Lake Nishi-no-ko connected to Lake Biwa-ko; 3: *Corbicula japonica* Prime, 1864, from Lake Shinji-ko; 4: *Corbicula japonica* Prime, 1864, from River Kushida-gawa; 5: *Corbicula japonica* Prime, 1864, from Lake Kahoku-gata; 6: *Corbicula japonica* Prime, 1864, from River Takase-gawa, Shirahama; 7: *Corbicula sandai* Reinhardt, 1878, from Lake Biwa-ko; 8: *Corbicula insularis* Prime, 1867, from a ditch in Sakae, Shirahama. Scale as 1 cm for 1–4 and 6–8, and as 2 cm for 5.

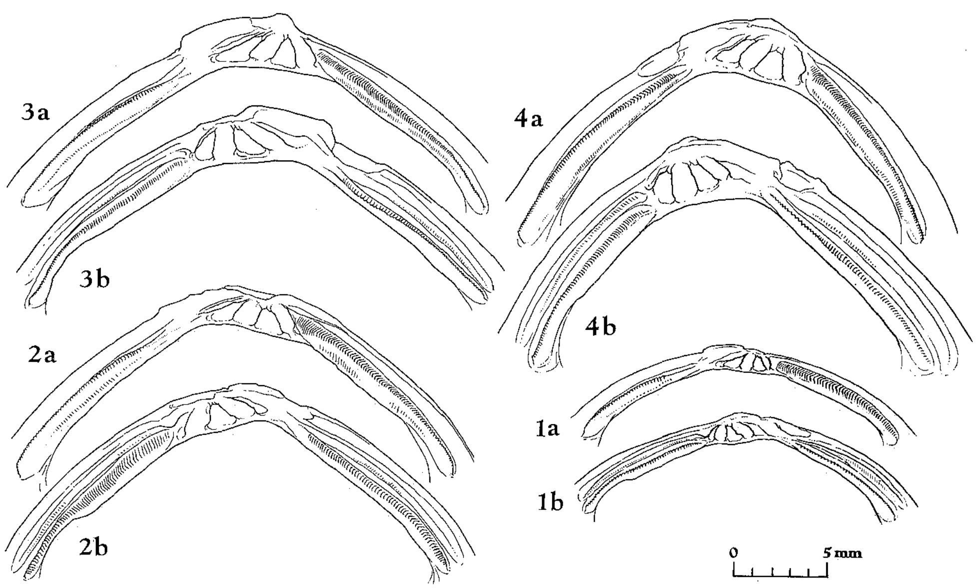


Fig. 2. Hinge plates, showing dentitions and lateral teeth, of three *Corbicula* species. 1: *C. leana*, Lake Nishi-no-ko, shell length 21.3 mm; 2: *C. japonica*, Shirahama, shell length 28.1 mm; 3: *C. japonica*, Lake Shinji-ko, shell length 31.3 mm; 4: *C. sandai*, Lake Biwa-ko, shell length 27.3 mm. a: left balve; b: right balve.

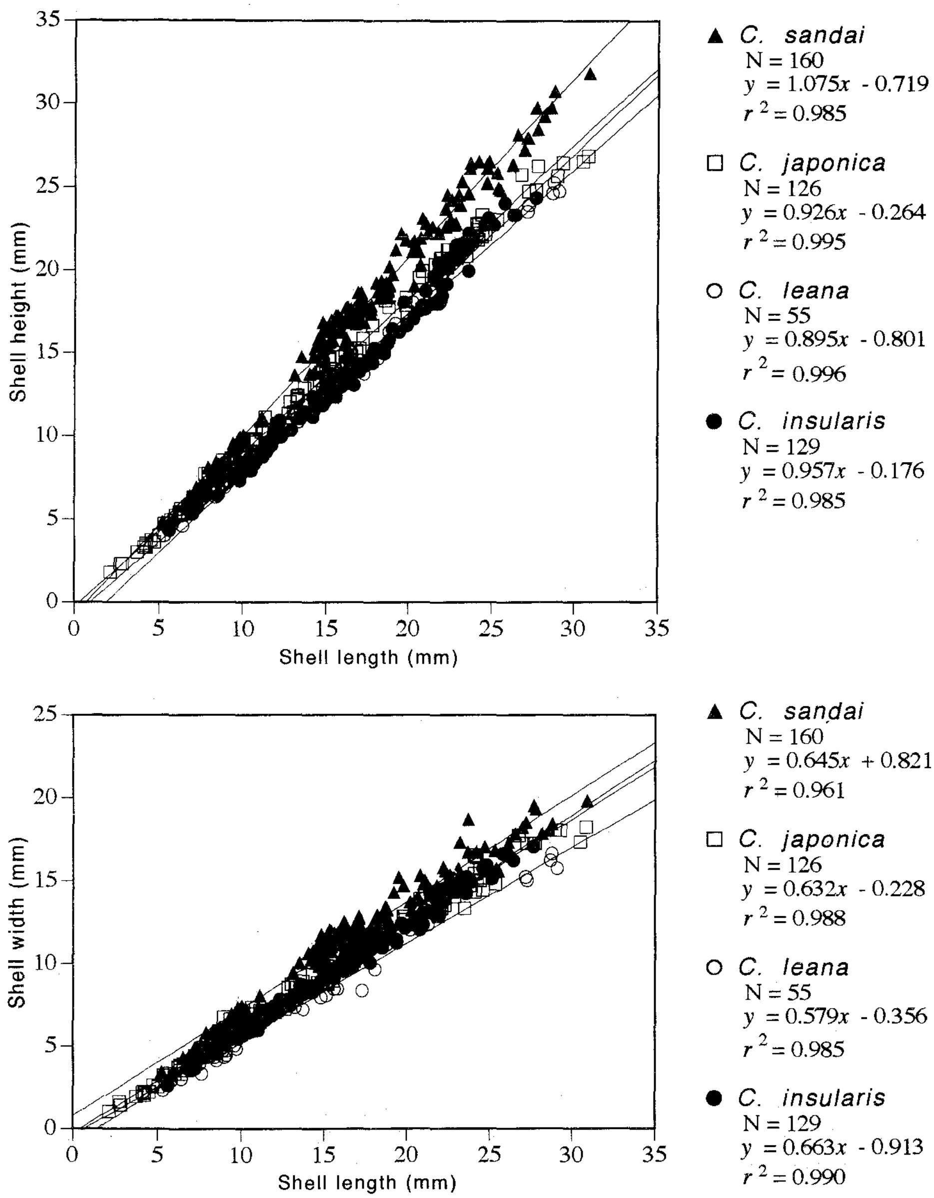
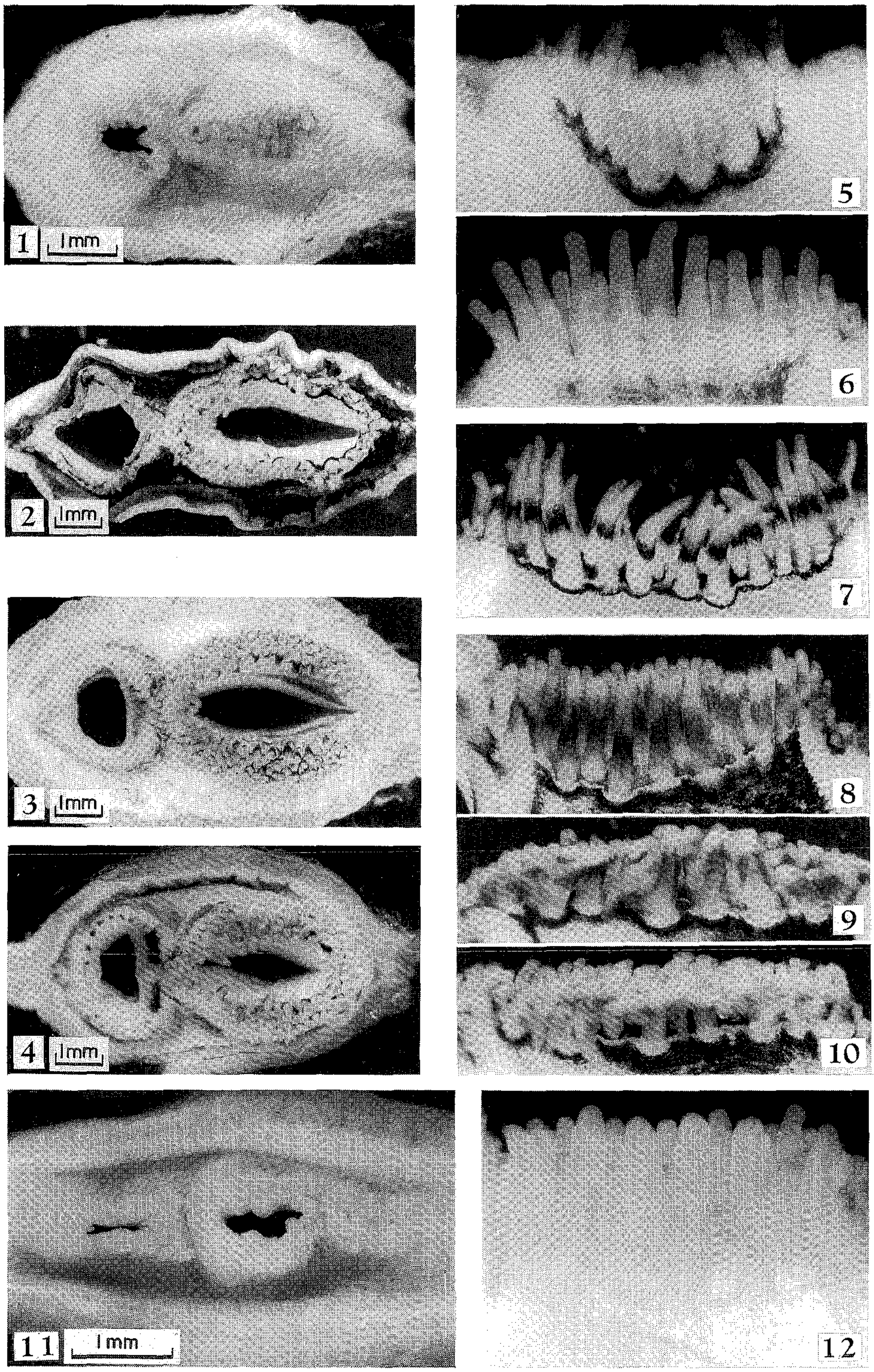


Fig. 3. Relationships between shell length and shell height (top) and between shell length and shell width (bottom) for four *Corbicula* species. *C. leana* and *C. japonica* are represented by a population from which the specimens of the widest range of size were availabe. *C. leana* from Shirahama; *C. japonica* from Lake Shinji-ko; *C. sandai* from Lake Biwa-ko; *C. insularis* from Shirahama. Symbols as indicated in the figure.


1
1mm
2
1mm
3
1mm
4
1mm
5
6
7
8
9
10
11
1mm
12

Siphons

The siphons of *Corbicula* are of Type B (Yonge, 1957, 1982). Britton & Morton (1979) illustrate diagramatically and compare the siphons of *C. fluminea* (Müller, 1774) and *C. fluminalis* (Müller, 1774). The siphons of the three Japanese species of *Corbicula*, as well as those of *C. insularis*, are similar to them in their general arrangement of the papillae (Fig. 4).

The exhalant siphon, dorsal to the inhalant siphon, has its aperture bounded by a naked muscular membrane and a ring of short papillae. These papillae represent the papillae of the middle fold of the mantle edge and are continuous with the rows of papillae on the fused middle folds of the dorsal mantle edges.

The inhalant siphon carries rows of papillae around its aperture. These inhalant siphonal papillae represent the marginal part of the inner fold of the mantle edge. No distinct ring of papillae representing the middle fold papillae is discernible, and the rows of papillae on the middle folds of the ventral mantle edges end in a cluster of short papillae on the fused middle folds ventral to the inhalant siphon.

The outer surface of the siphons and surrounding mantle groove are dark, or almost black in *C. japonica*, pale with weakly orange narrow stripes in a circumambient area of the inhalant siphonal papillae and along the fringe of the membrane bounding the exhalant aperture in *C. sandai*, but generally pale gray in *C. leana*. The inner surface of the inhalant siphon is furnished with a dark colour band around the bases of the papillae, which is darker in *C. japonica* and paler in *C. leana*. The differences in coloration partly conincide with the statements by Suzuki & Oyama (1943, p. 145) that the siphons are generally dark in Sectio *Corbicula* of Subgenus *Corbicula* of Genus *Corbicula*, whereas they are not dark in Sectio *Corbiculina* to which *C. leana* is assigned.

C. insularis is rather similar in coloration to *C. sandai*. The outer surface of the siphons and surrounding mantle groove are pale and weakly orange, and there is no dark pigmentation on the inner surface of the siphons and inhalant siphonal papillae.

Fig. 4. (on the opposite page) Siphons of four *Corbicula* species in external posterior view (1–4, 11) and inhalant siphonal papillae in inner view (5–10, 12); dorsal exhalant aperture on the left. 1: *C. leana*, Hatasho, Shiga, s.l. 23.0 mm; 2: *C. japonica*, Lake Shinji-ko, s.l. 28.0 mm; 3: *C. sandai*, Lake Biwa-ko, s.l. 25.0 mm; 4: *C. sandai*, Lake Biwa-ko, s.l. 25.0 mm; 5: *C. leana*, Gion, Okayama, s.l. 25.0 mm; 6: *C. leana*, Shirahama, s.l. 29.0 mm; 7: *C. japonica*, Lake Shinji-ko, s.l. 30.8 mm; 8: *C. sandai*, Lake Biwa-ko, s.l. 23.0 mm; 9: *C. sandai*, Lake Biwa-ko, s.l. 23.0 mm; 10: *C. sandia*, Lake Biwa-ko, s.l. 23.0 mm; 11: *C. insularis*, Shirahama, s.l. 27.4 mm; 12: *C. insularis*, Shirahama, s.l. 24.6 mm.

Inhalant Siphonal Papillae

Shape

Table 2. Summary of features of inhalant siphonal papillae in four *Corbicula* species.

Species and locality	Range of shell length (mm)	Number of specimens examined	Occurrence of Specimens bearing each type of papillae: solely simple	bases coalesced	branched (rami or knobs)	fused	Range of number of rows of papillae	Range of number of papillae on innermost row	Range of total number of papillae (solely simple)	Range of total number of tips of papillae
Corbicula leana										
Lake Nishi-no-ko	8–15	33	30	1	2	0	2–3	12–16	23– 66	37– 66
	15–22	20	15	0	5	1	2–3	13–20	45– 76	55– 76
Okayama	6–15	35	11	0	23	1	2–3	10–28	30– 47	23– 59
	15–22	15	4	4	9	0	1–3	12–24	19– 81	19– 81
Shirahama	7–15	20	18	1	1	0	2–3	10–15	22– 51	22– 54
	15–22	6	5	1	0	0	2–3	13–16	44– 57	44– 57
	22–31	16	15	0	1	0	2–3	14–22	50– 87	50– 87
Corbicula japonica										
Lake Shinji-ko	5–15	27	26	0	1	0	2–3	12–21	20– 64	20– 64
	15–22	11	8	1	1	1	2–4	14–22	71– 94	71–101
	22–31	32	23	3	6	1*	2–4	14–26	70–129	70–136
Shirahama	15–22	2	2	0	0	0	2–3	14–16	50– 61	50– 61
	22–29	8	5	2	1	0	2–3	10–20	68– 70	65– 84
Corbicula sandai										
Lake Biwa-ko	13–15	25	6	1	8	10	3–5	13–16	82–116	55–169
	15–22	47	5	1	38	11	4–6	13–18	104–181	91–377
	22–31	62	7	0	45	13	4–7	14–22	143–220	103–384
Corbicula insularis										
Shirahama	7–15	11	11	0	0	0	2–3	9–12	28– 42	28– 42
	15–22	8	8	0	0	0	2–3	11–18	49– 76	49– 76
	22–26	6	3	0	3	0	3	16–18	59– 74	59– 83
Corbicula fluminea										
Hong Kong (purple)	15–18	5	5	0	0	0	3–4	18–22	78–100	78–100
(white)	15–18	7	4	0	3	0	3–4	15–18	61– 73	61–105

* apparently anomalously fused into lump, partly deficient, and having only 22 tips almost in one row.

The inhalant siphonal papillae of several representative specimens of the four *Corbicula* species are shown in Figs. 4–8. Different forms of papillae are clearly noticeable, and the papillae can be separated into four types by their form: (a), simple, elongate finger-form, projecting separately from their base, without branches or knobs; (b), basally coalesced (adjoined) with others, otherwise simple; (c), branched, i.e., forming branches of some length in the distal part or knob-like accessory projections, producing multiple tips; (d), variously fused with others by branches, often forming a plate or a lump and obscuring tips and bases. In the fused papillae,

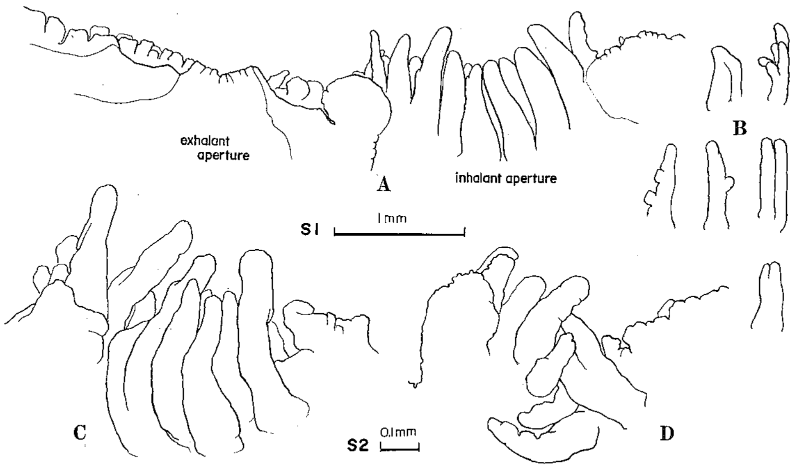


Fig. 5. Inhalant siphonal papillae of *C. leana* from Gion, Okayama. A: s.l. 25.0 mm, inhalant siphon on the right and exhalant siphon on the left; B: papillae of various shapes from different specimens; C: s.l. 9.4 mm; D: s.l. 6.3 mm. Scale S1 for A and B; scale S2 for C and D.

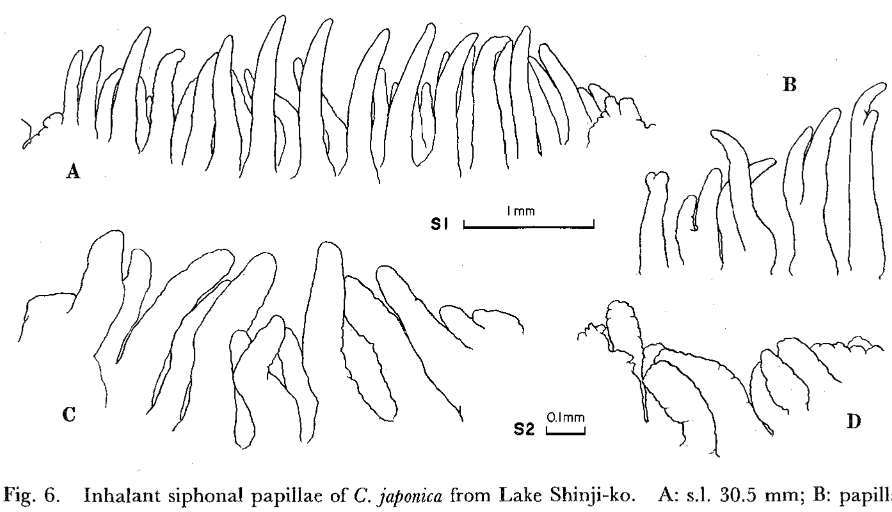


Fig. 6. Inhalant siphonal papillae of *C. japonica* from Lake Shinji-ko. A: s.l. 30.5 mm; B: papillae of various shapes from different specimens; C: s.l. 8.8 mm; D: s.l. 5.5 mm. Scale S1 for A and B; scale S2 for C and D.

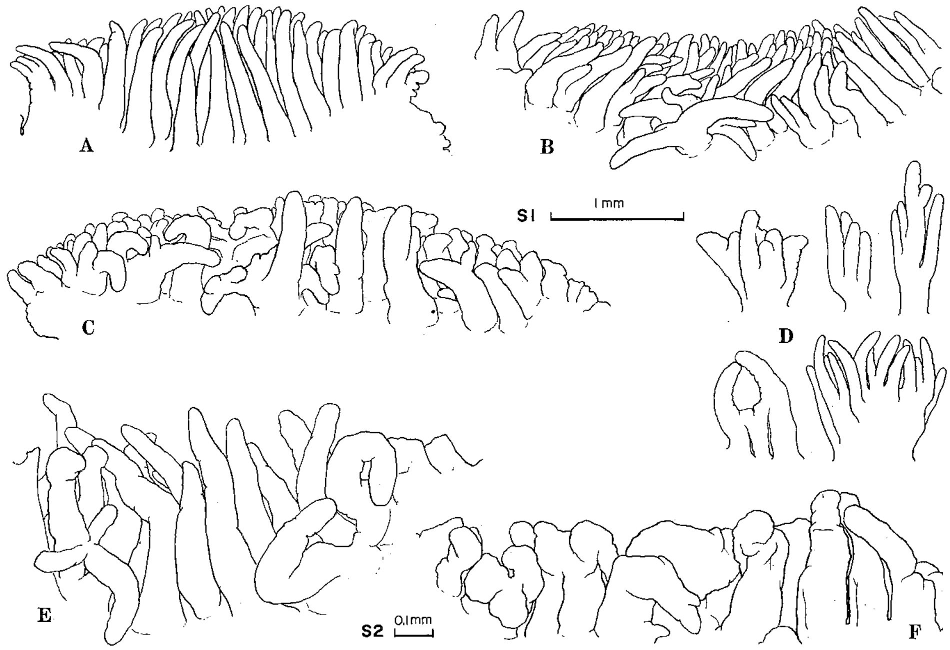


Fig. 7. Inhalant siphonal papillae of *C. sandai* from Lake Biwa-ko. A: s.l. 27.0 mm; B: s.l. 25.0 mm; C: s.l. 23.0 mm; D: papillae of various shapes from different specimens; E: s.l. 8.8 mm; F: s.l. 7.7 mm. Scale S1 for A-D; scale S2 for E-F.

Fig. 8. Inhalant siphonal papillae of *C. insularis* from Shirahama, Wakayama. A: s.l. 18.5 mm; B: s.l. 11.2 mm; C: s.l. 7.2 mm; D: a branched papilla. Scale S1 for A, B and D; scale S2 for C.

elevated heads may occur, that are counted as a tip. As a consequence, the number of tips is not necessarily smaller than that of the papillae. The results of our examination of the papillae of different types are summarized in Table 2.

In *C. leana* (Fig. 5), the inhalant siphonal papillae are predominantly simple in most samples, but a sample from a canal in Okayama comprised many specimens bearing papillae that were branched. Only in a few specimens, did a few basally coalesced papillae occur, and very rarely one or two fused ones.

The papillae of *C. japonica* (Fig. 6) are, as in *C. leana*, predominatly simple. The papillae with coalesced bases, knob-like projections or branches were found in a small number of specimens and fused papillae were extremely rare.

In *C. sandai* (Fig. 7), on the contrary, branched papillae and fused papillae are common, occurring in numbers in the majority of specimens, particularly larger specimens. Simple papillae are also commonly found in almost all specimens, but the specimens bearing solely simple papillae are the minority, irrespective of the size. Several examples of the numbers of the papillae and their tips in each row in a specimen are given in Table 3.

The inhalant siphonal papillae of *C. insularis* are predominantly simple, with the infrequent occurrence of simply forked papillae (Fig. 8).

Although the number of specimens examined was small, the inhalant siphonal papillae of *C. fluminea* are similar to those of *C. japonica* in the occurrence of types of papillae.

Disposition, Number and Coloration

The inhalant siphonal papillae are arranged in rows encircling the inhalant siphonal aperture (Fig.9). The rows are not always clearly serially distinguishable

Table 3. Examples of the numbers of inhalant siphonal papillae and their tips on each row in *Corbicula sandai*, from the innermost outward from left to right, and the total numbers on the right. Numbers of papillae below, and numbers of tips above the bar. Sizes of specimens in shell length.

Specimens bearing branched papillae	
23.7 mm	$\frac{18}{18}+\frac{29}{24}+\frac{38}{36}+\frac{43}{40}+\frac{61}{58}+\frac{19}{19}=\frac{208}{195}$
25.3 mm	$\frac{36}{17}+\frac{33}{20}+\frac{40}{28}+\frac{47}{39}+\frac{57}{50}+\frac{9}{9}=\frac{217}{163}$
25.5 mm	$\frac{21}{20}+\frac{26}{26}+\frac{30}{30}+\frac{49}{49}+\frac{60}{60}+\frac{23}{23}=\frac{209}{208}$
28.6 mm	$\frac{27}{17}+\frac{36}{18}+\frac{18}{15}+\frac{51}{37}+\frac{40}{33}+\frac{63}{53}+\frac{28}{28}=\frac{272}{201}$
Specimens bearing both branched and fused papillae	
24.7 mm	$\frac{16}{16}+\frac{11}{14}+\frac{26}{26}+\frac{31}{30}+\frac{60}{62}+\frac{7}{7}=\frac{151}{154}$
26.2 mm	$\frac{39}{19}+\frac{50}{26}+\frac{58}{48}+\frac{32}{25}+\frac{4}{4}=\frac{183}{122}$
27.0 mm	$\frac{23}{16}+\frac{22}{25}+\frac{27}{27}+\frac{33}{32}+\frac{45}{44}+\frac{8}{8}=\frac{158}{149}$

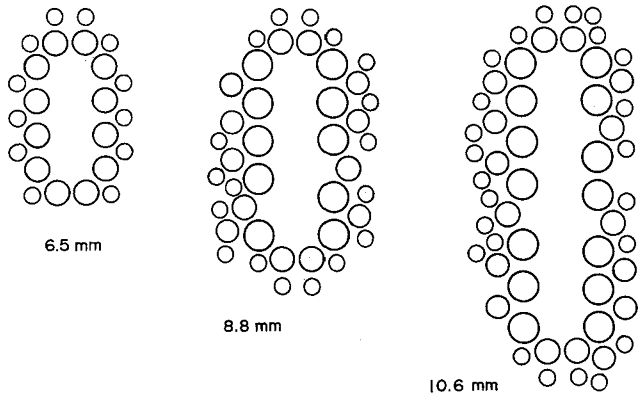


Fig. 9. Diagramatical representation of the change in disposition of inhalant siphonal papillae with size in *C. japonica* from Lake Shinji-ko.

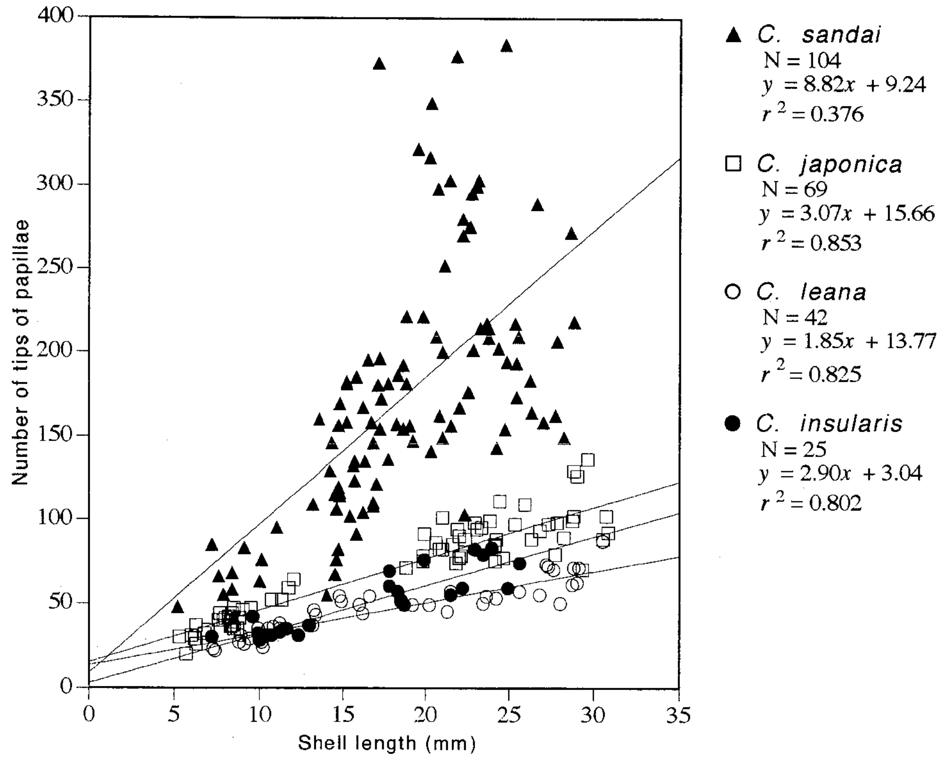


Fig. 10. Relationships between shell length and total number of tips of inhalant siphonal papillae in four *Corbicula* species. *C. leana* and *C. japonica* are represented by a population from which the specimens of the widest range of size were availabe. *C. leana* from Shirahama; *C. japonica* from Lake Shinji-ko; *C. sandai* from Lake Biwa-ko; *C. insularis* from Shirahama. Symbols as indicated in the figure.

from each other. The papillae in the innermost row are generally longer and larger than outer ones, which diminish in size outwards; outermost papillae are often short cones. The innermost papillae are distinctly coloured with a dark band in *C. japoncia*, and the bands are paler and wider in *C. sandai*, whereas in *C. leana* they are indistinguishably pale with a pair of dark spots on opposite sides of each papilla (Fig. 4).

The number of rows increases with size, and is larger in *C. sandai* and smaller in *C. leana* (Table 2). The number of papillae in each row differs with size and among the species, and the number of papillae on the innermost row is slightly smaller in *C. sandai* than in other species (Table 3). Since many of the papillae are branched variedly and the number of rows of papillae is larger in *C. sandai*, the total number of papillae tips is exceedingly larger in this species than in others (Fig. 10).

Discussion

Morphological Differences in Inhalant Siphonal Papillae

It is apparent from the results of our examination of the inhalant siphonal papillae that *C. sandai*, endemic to Lake Biwa-ko and its tributaries, is clearly distinctive from other species in having more numerous papillae, which are frequently fused with each other. This characteristic fusion of papillae is very rarely found in other species, and what is observed in *C. japonica* and *C. leana* is that two simple papillae are fused side by side partly or along most of their length in *C. japonica*. On the other hand, *C. leana* and *C. japonica* resemble each other in terms of the inhalant siphonal papillae, but can be distinguished in coloration and numbers. It should be noted that these differences are discernible in fairly small, young, individuals and can serve for the identification of the species, particularly *C. sandai*.

Morphological features of the soft body of *Corbicula* have little been treated. The siphonal morphology of *Corbicula* was first presented in a comparable way by Britton & Morton (1979). They showed that *C. fluminea* differed from *C. fluminalis* in the morphology of the siphon in the following respects: (1), possessing a band of pigment on the tentacles of the inhalant siphon; (2), possessing a ring of pigment internally in the exhalant siphon; (3), more densely pigmented externally in the exhalant siphon; (4), the number and relative size of the sensory tentacles around the exhalant siphon being less and (5), the papillae of the fused mantle folds dorsal and ventral to the siphon forming a single alternating row. They noticed that there was a high degree of intra-specific variation in the siphon, and presented composite diagrams of the siphons of *C. fluminea* and *C. fluminalis*. However, the features of the inhalant siphonal papillae are not mentioned in their paper.

Various forms of siphonal papillae have been reported upon for several bivalves; for example, pinnate papillae in Platyodon (Yonge, 1951), Siliqua (Yonge, 1952) and Petricola (Purchon, 1955; Yonge, 1957), and club-tipped papillae in Solen (Morton, 1984). If the inhalant siphonal papillae func-tion primarily as strainers to prevent undesirable large particles being inhaled, as Yonge (1957) suggests by calling them 'straining tentacles', branching of papillae is apparently effective and efficient, but coalescing and fused are not. The adaptive and functional meaning of the modified state of siphonal papillae encountered in *C. sandai* is wholly unknown.

Classification and Relationship of Japanese Species of *Corbicula*

Morton (1979) once urged "that the conchologist must be relegated to second place; a solution to *Corbicula* systematics will clearly not come from shell characters alone but only from associated soft part morphological studies" (p. 36). In this paper Morton claims that the Japanese species of *Corbicula* (involving *Corbiculina*) might be referrable to *C. fluminea* and *C. fluminalis*. Since his proposition of two species-complexes of Asiatic *Corbicula* has not been refuted and since most of the Japanese literature dealing with *Corbicula* taxonomy is in Japanese and is not known widely, a short review is not redundant, although it is not our intention to meddle in taxonomic discussion of the species.

Japanese species of the genus *Corbicula* have been variously classified and named. There were more than 10 species and subspecies nominally admitted (cf. Kuroda, 1938). Establishment and synonymization of species and subspecies reported from Japan created really a mess as Britton & Morton (1979) perceived in their taxonomic discussion of world-wide corbiculids.

Kira (1954), as mentioned by Morton (1979, p. 30; "1961" given here for Kira by him is the year of the publication of one of the prints of the enlarged and revised edition), was the first to list only three species of Japanese corbiculids. It is not, however, known if Kira really believed that *Corbicula* was represented only by these three species in Japan, since that kind of book did not usually intend to include all known species. Besides, Kira did not give any reference to synonyms, as was usually so in illustrated books. What Morton described for the synonymy of these species is, therefore, not attributable to Kira. Apparently, it is based on Table 1 of Miyazaki (1936), but it is not appropriate to consider it as a table of synonymy. There is not a trace of taxonomic discussion in Miyazaki's paper, and that table gives merely a grouping of contemporaneously admitted species in view of their habitat and breeding habits, if ever a taxonomist can use these characteristics in classification.

Extensive synonymization was actually proposed by Habe (1951). In this, he identified four species of *Corbicula* in Japan, and several more in neighbouring areas. However, the lists of synonyms given there did not include some of the names previously used, and the relevant characteristics distinguishing these four species were not discussed at all, as it was mostly so in past Japanese molluscan literature when some of the Japanese corbiculid species were synonymized with others or transferred to the subspecies of others. Habe (1977) further synonymized *C. awajiensis* to *C. leana* and founded the current recognition of three species of *Corbicula* in Japan, namely *C. japonica*, *C. sandai* and *C. leana*. The subgenus *Corbiculina* comprising *C. leana* was also raised to the generic level.

Identification of the Japanese species of *Corbicula* was severely criticized and radically altered by Morton (1979). His arguments were centred on the descriptions by Prashad (1928, 1929a,b, 1930) and were presumably literary issues, not based on actual specimens. Following the array of relationships stated for the species, he concluded that the Japanese species were attributable to *C. fluminea* and *C. fluminalis*. The same opinion was also expressed in Britton & Morton (1979). Not only the taxonomic status and nomenclature of the species, even the existence of three species was doubted, although Morton (1983) later wrote "A third species *C. sandai* Reinhardt, 1877, may be endemic to Lake Biwa" (p. 82), referring to Mori (1978). Morton (1986), however, expressed himself as still being strongly inclined to admit but two species of *Corbicula* in Japan. It should be added here that although the classification of Japanese *Corbicula* by Habe (1977) has been generally followed in the later studies in Japan, the propositions of Morton (1979, 1986) have never been considered, discussed or justified nor has any attention been paid in the Japanese literature. At the same time, Morton (1979) also doubted that *C. sandai* was non-incubatory but was releasing non-swimming veligers, by writing "How can this anomaly be possible?" Although his description is somewhat incorrect, it is really what *C. sandai* is doing (Hurukawa & Mizumoto, 1953; also Nishino's observation).

The presence of three forms of *Corbicula* in Japan has been recently confirmed independently from the shell morphometry by Takayasu *et al.* (1986) and from the karyological study by Okamoto & Arimoto (1986). The three forms are the species identified as *C. japonica*, *C. leana* and *C. sandai*. Takayasu *et al.* indicated through principal component analysis that the shape and arrangement of teeth could distinguish three species, particularly *C. sandai* from other two, being regarded useful in the study of fossils. The findings of Okamoto & Arimoto are more decisive, revealing karyotype difference among the three species. They examined the karyological relationship of the three and concluded that the ancestor of *C. japonica* gave rise to the ancestor of *C. sandai* with a reduced chromosome number, and from the latter originated the ancestor of triploid *C. leana*. The present results of this morphological study of the inhalant siphonal papillae also appear to support the recognition of three species of *Corbicula* in Japan.

As can be read from Appendix Table, *C. japonica* and *C. leana* have been confused through local forms. Conversely, *C. sandai* has been regarded as relatively distinct. The endemism of *C. sandai* to Lake Biwa-ko, which was once reported from streams and ponds in Kyoto that had connection with this lake, is undeniable, although attempts have been made to introduce it to some other lakes and lagoons in other districts with some success (Kuroda & Fujita, 1936). Lake Biwa-ko has been frequently noted as characterized by its climatic and geological conditions and by the fauna with many endemic species. Annandale (1922) described that the number of endemic species was large and "The Mollusca of Lake Biwa and its immediate neighbourhood are of particular interest and include in their numbers no less than thirty-four species --- sixteen Gastropods and eighteen Pelecypods --- nearly a quarter of the whole --- are apparently endemic in the lake" (p. 132). Which species he considered endemic was not indicated in his table, but *C. sandai* might not be included among them, since he wrote: "Among the species that occur as far north as Lake Biwa and no further are the sponge *Spongilla clementis*, the molluscs *Hydrobioides striatula* (represented by the Japanese race *japonica*), *Corbicula sandai* and *Sphaerium heterodon*, and several fishes" (p. 140). This concept of *C. sandai* had little influence on later views toward this species. Yagura (1922) considered that the corbiculid shells found in the remains of the Stone Age were *C. nipponensis* and *C. japonica* and that some of them were of the form comparable to *C. sandai*. From this, he speculated that *C. nipponensis* gave rise to *C. japonica* which in turn gave rise to *C. sandai*. Conversely, Kuroda & Fujita (1936) and Kuroda (1938) regarded *C. sandai* as belonging phylogenetically to the *leana* group, but later Kuroda (1947) admitted that the shell characteristics of *C. sandai* indicated its affiliation to the *japonica* group, without referring to his previous opinion.

The concept that endemic freshwater *C. sandai* has originated from brackish *C. japonica* as a marine relic during past geological periods has been advocated frequently by many scientists devoted to the study of Lake Biwa-ko. Kuroda (1947) suspected that *C. sandai* was an example of a land-locked organism. Thus, Uéno (1979) wrote: "The occurrence in Lake Biwa of such a boreal element of marine origin is of great zoogeographical interest. A similar view will also be applied to *Gasterosteus*, *Anisogammarus* and *Corbicula sandai*. The last-named bivalve which had originally been a brackish water inhabitant became adapted to the freshwater habitat and quite changed even its reproductive process." Coupled with the geological history of the district, Ishida (1976) explained that *C. sandai* was regarded to have differentiated around 800 thousands years ago from *C. japonica* in ancient Osaka Bay which invaded inland, and this assumption was followed by many later scientists.

The view presented by Okamoto & Arimoto (1986) concerning the relationships among the three species (opt. cit.) is, in contrast, quite different. They suppose that, taking into consideration the continental species together, *C. sandai* might be derived from the one which was once widely distributed in the freshwater areas over the region, from which *C. leana* originated, and then restricted to Lake Biwa-ko in Japan. Okamoto (1994) repeated the same view. The identity of *C. sandai* and the form inhabiting Lake Tai-Hu in China has sometimes suspected by some scientists, e.g. Annandale (1918), Liu *et al.* (1980) and Miyadi (1980). Considering the occurrence of *C. sandai* and its supposed ancestral form ('*sandaigenes*' or sp. B) in the fossil malacofaunas of the Pliocene and Pleistocene in the surrounding areas of Lake Biwa-ko, and also referring to the views of Ishida and of Liu *et al.*, Matsuoka (1987) upheld the assertion that *C. sandai* was one of the paleoendemic.

Whichever of the suppositions is correct, it must be admitted that strongly modified and variable inhalant siphonal papillae in *C. sandai* seem apomorphic in comparison with simple papillae, suggesting *C. sandai* to be a specialized form. Further examination of other new features, possibly molecular traits, is needed to discuss the evolutionary relationship among the three species, and other species as well.

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References

Annandale, N. 1918. Zoological results of a tour in the Far East. The mollusca of Lake Biwa, Japan. Mem. Asiat. Soc. Bengal, 6: 41–74, Pl. III.

———. 1922. The macroscopic fauna of Lake Biwa. Annot. Zool. Japon., 10(5): 127–153.

Britton, J.C. & Morton, B. 1979. *Corbicula* in North America: the evidence reviewed and evaluated. In: J.D. Britton (ed.), Proceedings of the First International Corbicula Symposium, Texas Christian University, Fort Worth, Texas 1977: 249–287. Texas Christian University Research Foundation, Fort Worth.

Habe, T. 1951. Genera of Japanese Shells. Pelecypoda No. 2. Kairui Bunken Kanokai, Kyoto, 186 pp. (in Japanese)

———. 1977. Systematics of Mollusca in Japan. Bivalvia and Scaphopoda. Zukan-no-Hokuryukan, Tokyo, xiii+372 pp. (in Japanese)

Hurukawa, M. & Mizumoto, S. 1953. An ecological studies on the bivalve "Setasijimi", *Corbicula sandai* Reinhardt of the Lake Biwa II. On the development. Bull. Japan. Soc. Sci. Fish., 19: 91–94. (in Japanese)

Ishida, S. 1976. Significance of paleoecological study on Lake Biwa-ko. In: Geological Society of Japan & Palaeontological Society of Japan (eds.), Monograph on Palaeoecology I: 42–62. (in Japanese)

Kawashima, T., Yamane, Y. & Yamamoto, K. 1985. Growth of *Corbicula japonica* in River Kando and morphological difference from *Corbicula japonica* in Lake Shinji-ko. Report from Fisheries Research Station of Shimane Prefecture, 5:94–102. (in Japanese)

Kira, T. 1954. Coloured Illustrations of the Shells of Japan. Hoikusha, Osaka, 172+24 pp, 67 Pls. (in Japanese)

Kuroda, T. 1938. Studies on Japanese *Corbicula*. Venus, 8(1): 21–36. (in Japanese)

———. 1947. Freshwater molluscs of Lake Biwa-ko. Yumehamaguri, Kairui Kenkyu, 17:170–175. (in Japanese)

——— & Fujita, T. 1936. *Corbicula sandai* raised in Lake Suwa-ko. Venus, 6(1): 60–63. (in Japanese)

Liu, Y., Zhang, W. & Wang, Y. 1980. Bivalves (Mollusca) of the Tai Hu and its surrounding waters, Jiangsu Province, China. Acta Zool. Sinica, 26(4): 365–369.

Masuda, O. & Habe, T. 1988. *Corbicula insularis* Prime established in Kurashiki City, Okayama Pref., Honshu. The Chiribotan (Newsletter of the Malacological Society of Japan), 19(2): 39–40. (in Japanese)

Matsukuma, A. 1986. Corbiculidae. In: Okutani, T. (ed.), Mollusca, Illustrations of Animals and Plants 8: 325. Sekai Bunka-sha, Tokyo. (in Japanese)

Matsuoka, K. 1987. Malacofaunal succession in Pliocene to Pleistocene non-marine sediments in the Omi and Ueno Basins, central Japan. J. Earth Sci. Nagoya Univ., 35(1): 23–115.

Miyadi, D. 1980. Corbiculids in Lake Tai-Hu and *Corbicula sandai* in Lake Biwa-ko. An article in the issue of September 4th, 1980, the Mainichi Newspaper. (in Japanese)

Miyazaki, K. 1936. On the development of bivalves belonging to the genus *Corbicula*. Bull. Japan. Soc. Sci. Fish., 5: 249–254.

Mori, S. 1978. Seventh report of the regular limnological survey of Lake Biwa (1973), III. Benthos. Mem. Fac. Sci., Kyoto Univ., Ser. Biol., 7: 11–29.

Morton, B. 1979. *Corbicula* in Asia. In: J.D. Britton (ed.), Proceedings of the First International *Corbicula* Symposium, Texas Christian University, Fort Worth, Texas 1977: 15–38. Texas Christian University Research Foundation, Fort Worth.

———. 1983. The sexuality of *Corbicula fluminea* (Müller) in lentic and lotic waters in Hong Kong. J.

moll. Stud., 49: 81–83.
———. 1984. Siphonal autotomy in *Solen corneus* (Bivalvia: Solenoidea) from Hong Kong. Malacol. Rev., 17: 95–96.
———. 1986. *Corbicula* in Asia: an updated synthesis. Amer. Malacol. Bull., Spec. Ed. 2: 113–124.
Okamoto, A. 1994. Origin of *Corbicula sandai*. In: Research Group for Natural History of Lake Biwa (ed.), The Natural History of Lake Biwa: 163–168. Yasaka-shobo, Kyoto. (in Japanese)
——— & Arimoto, B. 1986. Chromosomes of *Corbicula japonica*, *C. sandai* and *C.* (*Corbiculina*) *leana* (Bivalvia: Corbiculidae). Venus, 45(3): 194–202.
Prashad, B. 1928. Revision of the Asiatic species of the genus *Corbicula*. I.--The Indian species of *Corbicula*. Mem. Indian Mus., 9: 13–27, Pls. 3–4.
———. 1929a. Revision of the Asiatic species of the genus *Corbicula*. II.--The Indo-Chinese species of the genus Corbicula. Mem. Indian Mus., 9: 29–48, Pls. 5–6.
———. 1929b. Revision of the Asiatic species of the genus *Corbicula*. III.--The species of the genus *Corbicula* from China, south-eastern Russia, Tibet, Formosa, and the Philippine Islands. Mem. Indian Mus., 9: 49–68, Pls. 7–8.
———. 1930. Revision of the Asiatic species of the genus *Corbicula*. IV.--The species of the genus *Corbicula* from the Sunda Islands, the Celebes and New Guinea. Mem. Indian Mus., 9: 193–203, Pls. 24–26.
Purchon, R.D. 1955. The functional morphology of the rock-boring lamellibranch *Petricola pholadiformis* Lamarck. J. mar. biol. Assoc., U.K., 34: 257-
Suzuki, K. & Oyama, K. 1943. Üerblick —ber die Corbiculiden Ostasiens (Materialien zur Monographie der ostasiatischen Corbiculiden 1). Venus, 12(3/4): 138–149. (in Japanese with German summary)
Takayasu, K., Urushido, T. & Okude, F. 1986. Comparative shell morphology of three species of Japanese Corbiculinae. Geol. Rept. Shimane Univ., 5: 35–42. (in Japanese)
Uéno, M. 1975. Evolution of life in Lake Biwa -- a biogeographical observation. In: S. Horie (ed.), Paleolimnology of Lake Biwa and the Japanese Pleistocene, Vol. 3: 5–13.
Yagura, W. 1922. Essays on Molluscs. Maruzen, Tokyo. 14+4xx+16 pp. (in Japanese)
Yonge, C.M. 1951. Studies on Pacific coast molluscs. II. Structure and adaptations for rock boring in *Platyodon cancellatus* (Conrad). Univ. Calif. Publ. Zool., 55(7): 401–408.
———. 1952. Observations on *Siliqua patula* Dixon and on evolution within the Solenidae. Univ. Calif. Publ. Zool., 55(9): 421–438.
———. 1957. Mantle fusion in the Lamellibranchia. Pubbl. Sta. Zool. Napoli, 29:151–171.
———. 1982. Mantle margins with a revision of the siphonal types in the Bivalvia. J. moll. Stud., 48: 102–103.

Appendix Table. List of names for the three Japanese species of *Corbicula*, used in taxonomic works by various authors.

Corbicula leana Prime, 1864

leana : Prime (1864), original description; Martens (1877); Kobelt (1879); Pilsbry (1907); Iwakawa (1909), Japanese name 'ma-shijimi'; Yagura (1922); Prashad (1924); Hirase (1927); Taki (1933); Hirase (1934); Kuroda (1938); Hirase & Kuroda (1949); Hirase & Taki (1951); Habe (1951); Kira (1954); Kuroda & Habe (1965); Okutani & Habe (1975); Matsukuma (1986).

leana orthodonta : Yagura (1922); Hirase (1934).

leana awajiensis : Habe (1951).

leana straminea : Okutani & Habe (1975), Japanese name 'awaji-shijimi'.

straminea : Martens (1877); Reinhardt (1878); Kobelt (1879); Pilsbry (1895); Prashad (1924).

straminea awajiensis : Prashad (1924).

pexata : Reinhardt (1878); Kobelt (1879).

awajiensis : Pilsbry (1901); Pilsbry (1907); Iwakawa (1909); Yagura (1922); Hirase (1927); Hirase (1934); Kuroda (1938); Hirase & Kuroda (1949); Hirase & Taki (1951).

orthodonta : Pilsbry (1907); Iwakawa (1909), Japanese name 'narihira-shijimi' or 'okura-shijimi'.

Corbiculina leana : Habe (1977).

Corbicula japonica Prime, 1864

japonica : Prime (1864), original description; Kobelt (1879); Pilsbry (1895); Iwakawa (1909), Japanese name 'yamato-shijimi'; Pilsbry (1907); Yagura (1922); Prashad (1924); Hirase (1927); Taki (1933); Hirase (1934); Kuroda (1938); Hirase & Kuroda (1949); Hirase & Taki (1951); Habe (1951); Kira (1954); Kuroda & Habe (1965); Habe (1977); Okutani & Habe (1975); Matsukuma (1986).

japonica sadoensis : Taki (1933); Hirase (1934); Kuroda (1938).

japonica delicata : Taki (1933).

japonica nipponensis : Hirase (1934).

japonica nipponensis forma *delicata* : Hirase (1934).

japonica transversa : Kuroda (1938), Japanese name 'chikugo-shijimi'.

japonica atrata : Kuroda (1938), Japanese name 'nihon-shijimi'.

japonica forma *martensi* : Oyama (1943); Hirase & Taki (1951).

japonica forma *sadoensis* : Hirase & Kuroda (1949).

japonica forma *delicata* : Hirase & Taki (1951).

biformis : Reinhardt (1877); Martens (1877); Reinhardt (1878).

ovalis : Reinhardt (1877); Reinhardt (1878).

transversa : Martens (1877); Kobelt (1879); Iwakawa (1897); Prashad (1924).

yokohamensis : Sowerby (1877).

fuscata var. *atrata* : Reinhardt (1878).

martens : Clessin (1878); Kobelt (1879); Pilsbry (1895).

reiniana : Clessin (1878); Kobelt (1879).

doenitziana : Clessin (1878); Kobelt (1879).

sadoensis : Pilsbry (1901); Pilsbry (1907); Iwakawa (1909), Japanese name 'sado-shijimi'.

nipponensis : Pilsbry (1907); Iwakawa (1909); Yagura (1922).

nipponensis delicata : Pilsbry (1907); Iwakawa (1909), Japanese name 'himenihon-shijimi'; Yagura (1922).

nipponensis sadoensis : Yagura (1922).

sandai : Pilsbry (1907), from Sendai-gawa, Satsuma (=Kagoshima Pref.), misidentification of local form of *japonica* ; Yagura (1922), Japanese name 'satsuma-shijimi'.

sp. (Japanese name 'chikugo-shijimi') : Iwakawa (1909); Yagura (1922).

atrata : Prashad (1924).

leana : Prashad (1924), synonymous to *reiniana*.

leana sadoensis : Prashad (1924).

Corbicula sandai Reinhardt, 1878

sandai : Reinhardt (1878), original description; Kobelt (1879); Iwakawa (1897); Iwakawa (1909); Yagura (1922); Prashad (1924); Hirase (1927); Taki (1933); Hirase (1934); Kuroda (1938); Hirase & Kuroda (1949); Hirase & Taki (1951); Habe (1951); Kira (1954); Kuroda & Habe (1965); Okutani & Habe (1975); Habe (1977); Matsukuma (1986).

sandai viola : Yagura (1922); Taki (1933); Hirase (1934).

sandai forma *viola* : Hirase & Taki (1951).

viola : Pilsbry (1907); Iwakawa (1909), Japanese name 'murasaki-shijimi'.